PAPERS READ.

On the Structure of the Paired Fins of *Ceratodus*, with remarks on the general theory of the Vertebrate Limb.

By William A. Haswell, M.A., B.Sc.

[Plate I.]

In his description of *Ceratodus Forsteri*,* Dr. Günther says respecting the fins:

"The limbs consist of two pairs of paddles similar in appearance to the termination of the tail; viz., a longitudinal axis, formed by the endoskeleton and muscles and covered with scales is surrounded by a broad rayed fringe. These paddles are structurally identical with the fins of *Lepidosiren*: only the axis and also the fringe are much dilated.

"The paddle is joined to the scapular arch by an elongate flattish, slightly curved cartilage; its proximal end has a glenoid cavity fitting into the humeral condyle; the joint is simple, free, allowing of a considerable amount of motion, its parts being held together by a ligament fastened around its circumference. This is the only true joint in the limb, all the other parts being fixed to one another by connective tissue. I consider this cartilage to be the forearm; a horizontal section along its longitudinal axis does not shew any primary division. The next following cartilage forms the base of the paddle; although externally it appears as a single flat broad short piece, unevennesses of its surface indicate that several primary pieces are coalesced in it."

"I am confirmed in this view by a horizontal section, in which the lines of the former divisions are preserved in the shape of tracts of a white connective tissue. Three such divisions may be distinguished corresponding to the three carpals of most Plagiostomes. If this determination is correct, then the antibrachial

* Phil. Trans. 1871.

cartilage just described is not represented in that order. The remaining framework of the paddle shews an arrangement unique among the Vertebrata. From the middle of the basal cartilage a series of about twenty-six quadrangular pieces takes its origin, forming a longitudinal axis along the middle of the paddle to its extremity. The pieces gradually become smaller and are scarcely distinguishable towards the end of the paddle. On the two posterior corners of each piece a branch is inserted running obliquely backwards towards the margin of the fin; the branches of the first eight or twelve pieces are three-jointed, the remainder two-jointed, the last having no branch at all. Slight irregularities, such as the origin of two branches from one side of a central piece occur, as also several four-jointed branches immediately on the basal cartilage."

On this description Huxley* makes the following comments:—

"In general, this description suits the pectoral fins of the specimen I have described very well. Mine, however, has only twenty median cartilages. All but the very last bear lateral rays; but towards the distal end of the fin these become minute, and consist of a single piece. Moreover the distal joints are much more slender, especially the last. A more important point is that the second shews no trace of such divisions as those described by Dr. Günther. To make sure of this I made a thin microscopic section of this cartilage on the right side, and thereby satisfied myself of the homogeneity of the cartilage of which it is composed."

"I find no true joint between the proximal median piece and the scapular arch, the connection between the two being effected by a solid fibrous mass."

Fig. 2 is copied from Huxley's figure of the pectoral fin of *Ceratodus*.

* P.Z.S., 1876, p. 46.

It will thus be seen that both Günther and Huxley, while their descriptions differ in various minor points connected with the arrangement of the cartilages, agree in regarding the fin of *Ceratodus* as essentially uniaxial, *i. e.* consisting of a single jointed axis, with the preaxial and postaxial sides of which a series of jointed cartilaginous rays are connected.

A similar, though simpler, arrangement had already been described as characterising the fin of *Lepidosiren*, and before the discovery of *Ceratodus*, Gegenbaur had come to the conclusion from theoretical considerations that the fundamental type of the Vertebrate limb very much resembled the fin of *Lepidosiren*. This primitive limb he designated the *archipterygium*, and in connection with it he remarks in the second edition of his "Grundriss der Vergleichenden Anatomie" (F. Jeffrey Bell's Transl. 1878, p. 473)—"When simplest this (the skeleton of the free part of the limb), is made up of cartilaginous rods (rays), which differ in their size, segmentation and relation to one another. One of these rays is larger than the rest and has a number of other rays attached to its sides. I have given the name of Archipterygium to the ground form of the skeleton which extends from the limb-bearing girdle into the free appendage. The primary ray is the stem of this archipterygium, the character of which enables us to follow out the lines of development of the skeleton of the appendage. Cartilaginous arches beset with rays form the branchial skeleton. The form of skeleton of the appendages may be compared with them; and we are led to the conclusion that it is possible that they may have been derived from such forms. In the branchial skeleton of the *Selachii* the cartilaginous bars are beset with simple rays. In many, a median one is developed to a greater size. As the surrounding rays become smaller, and approach the larger one, we get an intermediate step towards that arrangement in which the larger median ray carries a few smaller ones. This differentiation of one ray, which is thereby raised to a higher grade, may be con-

nected with the primitive form of the appendicular skeleton; and, as we compare the girdle with a branchial arch, so we may compare the median ray and its secondary investment of rays with the skeleton of the free appendage."

"All the varied forms which the skeleton of the free appendages exhibits may be derived from a ground-form which persists in a few cases only, and which represents the first, and consequently the lowest, stages of the skeleton of the fin—the Archipterygium. This is made up of a stem which consists of jointed pieces of cartilage, which is articulated to the shoulder-girdle, and is beset on either side with rays which are likewise jointed. In addition to the rays on the stem there are others which are directly attached to the limb-girdle."

"*Ceratodus* has a fin-skeleton of this form; in it there is a stem beset with two rows of rays. But there are no rays on the shoulder girdle. This biserial investment of rays on the stem of the fin may also undergo various kinds of modifications. Among the *Dipnoi*, *Protopterus* retains the medial row of rays only which have the form of fine rods of cartilage; in the *Selachii*, on the other hand, the lateral rays are considerably developed."

Thus both Gegenbaur and Huxley regard the fin of *Ceratodus* as representing or nearly representing a primitive type from which the limbs of the *Ganoids*, the *Holocephali*, and the *Selachii* have been derived. Reasons have already been adduced by Balfour,* Thacker and others, for dissenting from this conclusion, and these, together with the facts which I am about to bring forward, seem to me to place it beyond a doubt that the limb of *Ceratodus*, so far from representing a primitive and generalised type, is, as indeed we should expect from various other points in the organisation of the animal, in reality highly specialised, and

* Comparative Embryology, Vol. ii., p. 506; "On the Development of the Paired Fins of the Elasmobranchii," etc., P.Z.S., 1881, p. 656.

is to be regarded as *derivable from* such simpler limb-skeletons as those of the *Selachii*.

In his work on the "Development of Elasmobranch Fishes" and in his "Comparative Embryology" F. M. Balfour gives an account of the development of the fins of Scyllium, which is important as throwing considerable light upon this question. Externally each fin first shews itself as a ridge of epiblast, subsequently enclosing mesoblast; the front and hind fins of each side are connected at first in some *Elasmobranchs* by a very low ridge of epiblast cells; but this connecting ridge soon disappears. Its existence, however, at this early stage would seem to render it probable, as pointed out by Balfour, that the pectoral and pelvic fins of each side had originally the form of a continuous fold similar in nature to the unpaired fins. The first rudiment of the skeleton of the fin consists of a bar of cartilage attached in front to the limb-arch and running backwards parallel with the long axis of the body; and a plate which extends into the fin and very soon becomes divided into a series of cartilaginous rods placed at right angles to the longitudinal bar. By a series of changes which are greater in the pectoral than in the pelvic fins, and include in the former the rotation outwards of the basal bar or *basipterygium* which becomes converted into the *metapterygium*, and the introduction of additional basal elements, the primitive longitudinal bar and segmented plate become converted into the skeleton of the adult fin.

The most important result of these researches, as regards the present question, was the proof that the paired fins are developed from structures which are essentially very similar to the unpaired fins. More recently Mivart* in a memoir entitled "On the Fins of Elasmobranchs, with Considerations on the Nature and Homologues of Vertebrate Limbs" (Trans. Zool. Soc., vol. x.) has endeavoured to shew that this fundamental identity of the

* And independently J. K. Thacker in a memoir on the Median and Paired Fins in the Transactions of the Connecticut Academy

paired and unpaired fins might have been inferred from their adult structure as well as from their mode of development.

Both Günther and Huxley, as already noted, found both the pectoral and pelvic fins to be uniaxial. I was surprised, therefore, to find that the skeleton of the pectoral fin of the first of two specimens very kindly placed at my disposal by Mr. Ramsay, presented the arrangement shewn in fig. 1.

There is first an elongate basal joint attached to the shoulder-girdle; upon this follows a short transversely oblong joint and to the distal border of this in turn are connected (1) a series of five post-axial rays, (2) the main axis of the paddle consisting of a series of cartilaginous joints to most of which are attached a pair of jointed cartilaginous rays, and (3) a supplementary axis (pre-axial fin-ray of Huxley) consisting only of four joints, and having only two rudimentary rays, one attached to the anterior and distal angle of the first joint, and the other to the same point on the second. The fin of the opposite side presented the same arrangement of the cartilaginous elements, except that the anterior axis had only one rudimentary ray in place of two. On examining the pectoral fins of a second specimen of *Ceratodus* I found that the anterior axis of neither of them had any rudiments of rays.

When the left pelvic fin of the first specimen was examined, a still greater divergence from the archipterygial type of structure presented itself. Articulating with the basal joint are (1) in front two small cartilages of irregular shape, the anterior of which supports a short ray, and (2) a broad, somewhat oblong plate. This plate is seen on a closer inspection to present traces of longitudinal division into two parts and is formed apparently by the partial coalescence of the bases (1) of a short bifurcated ray, (2) of a short branching anterior axis supporting five rays, (3) of the basal undivided portion of the main axis, and (4) of a short posterior axis giving off one simple and two bifurcated branches. Of the rays attached to the distal portion of the axis

several are bifurcated. The pelvic fin of the opposite side of the same specimen (fig. 4) has a totally different structure and very closely resembles the pectoral fins. There is a broad second joint divided distally by a fissure, the posterior division being connected distally with the main axis of the fin and supporting posteriorly three short rays, while the anterior forms the base of stout anterior ray or unbranched anterior axis. None of the rays in this fin are branched and the arrangement approaches very closely to that figured and described by Günther (fig. 3.). The pectoral fins of the second specimen are very similar to those of the first, except that the anterior axis gives off no branches. The left pelvic fin of this specimen (fig. 6) somewhat resembles that of the first, but there are important differences in detail. Thus the anterior axis is much longer and more complexly branched, and the main axis itself subdivides into two, only one of which, however, is continued to the extremity of the fin. The right fin (fig. 7), is very similar to the left fin of the first specimen with some slight points of difference which hardly require description.

As Günther and Huxley each examined two specimens, this branching of the cartilaginous skeleton of the fin of *Ceratodus* would appear to be an exceptional arrangement; and it is reasonable to regard it as an instance of atavism, and as pointing back to a pre-existing condition in which the fin-skeleton consisted of branching jointed cartilaginous elements supporting a cutaneous expansion considerably broader than that of the fin of the living *Ceratodus Forsteri*. The second joint seems to be formed by the coalescence of the bases of several of the main ribs or axes of the fin, and the first joint is to be regarded as derived from the equivalent of the *basipterygium* of the embryonic *Scyllium*. In the absence, however, of any data on the development of *Ceratodus* the homologies of these cartilages cannot be determined with any certainty, but the varieties of arrangement which I have described seem to point to the above conclusion.

If these cases of plurality of axes in the limb are cases of atavism, then they may perhaps point back to a common form of fin-skeleton whence the normal specialised fin of *Ceratodus* and the *cheiropterygium* of the higher vertebrates may have been derived. The speculations of Prof. Huxley (*l. c.*, p. 56) would however, require little modification to adapt them to such a biaxial or multi-axial type of limb, and it would be idle, in view of the variations which I have shewn the fin-skeleton to present, to offer any further more detailed suggestions in this direction.

If we were to speculate as to the nature of the earliest fin-skeleton, we should most probably, in view of the structure of the embryonic fin in the Elasmobranchii, come to the conclusion that at first it consisted of a series of detached nodules of cartilage; that, as muscular action became more definite in direction, these nodules came to be arranged in rows so as to assume the form of numerous parallel, jointed rods of cartilage, which might coalesce in some cases so as to form a continuous plate; the coalescence of the bases of these jointed rays as the two pairs of fins became differentiated from one another and the proximal part of each fin became narrowed, and the inward growth of this, probably, as Thacker has suggested, formed the *basipterygium*. As the breadth of the whole fin became decreased to form the narrow, pointed paddle of *Ceratodus*, the jointed rods became approximated not only at their bases but throughout a considerable portion of their length, and their partial coalescence resulted in the formation of a branching structure, the branches of which, as centralisation went on further, came to be arranged on each side of a single stem—the axis of the so-called *archipterygium*.

A study of the soft parts of the fin in *Ceratodus* points to the same conclusion as the consideration of the skeleton. The pectoral fin of *Ceratodus* as observed by Mr. E. P. Ramsay, is capable of somewhat complex movements, and to accomplish those the muscles, though simply arranged, are somewhat more

highly specialised than in even the adult Dog Fish or Ray. In these the muscles which move the fin are flat plates made up of coarse fasciculi radiating from the limb arch to the bases of the fin rays.

In *Ceratodus* there is a strong extensor muscle arising from the shoulder-girdle and inserted along the dorsal surface of the basal joint, the next joint, and the first two joints of the central axis; and a flexor muscle with a similar arrangement but interrupted opposite the distal end of the basal joint, the distal portion of its fibres chiefly having their proximal attachment with the tubercle at the distal end of the ventral surface of the basal cartilage. Along the axis of the fin both on the dorsal and the ventral surfaces run a series of interrupted muscular fasciculi which pass between adjacent joints of the axis and the basal joints of the rays, and passing obliquely outward from those are series of fibres connected externally with the bases of the fin-rays. The front portion of the extensor turns round the anterior margin so that it acts to some extent as an abductor. Beneath it are two muscles, one arising from the shoulder girdle and inserted wholly into the basal cartilage; and the other arising from a prominent tubercle near the distal end of that cartilage, its fibres passing in a radiating manner to be inserted into the next joint and the two basal joints of the anterior axis; this muscle must act as a rotator.

In *Ceratodus*, as in all limb-bearing vertebrates, the nerves which supply the limbs converge from an extent of the spinal cord which is great compared with the breadth of attachment of the limb. In *Ceratodus* the pectoral fin for example is supplied by a single nerve-trunk to which fibres from four spinal nerves contribute. After passing the axil of the limb this main trunk divides into two, one of which turns round the anterior border of the fin to the dorsal surface, while the other runs straight onwards along the middle of the ventral surface.

If the primordial limb consisted of a wide fold flanking a number of vertebral segments, as seems highly probable from

Balfour's researches, it would naturally be supplied by branches from most of the spinal nerves belonging to those segments; and, as the base of connection of the fin with the body became narrowed, these nerves would be brought into closer connection with one another, and would assume the appearance of converging towards the axil of the limb. The fact that the nerves which go to supply the limbs originate from a number of spinal nerves would thus seem to afford an additional argument in favour of this view of the origin of limbs, and against the theory put forward by Gegenbaur that the limbs are modified branchial arches.

Explanation of Plate I.

Fig. 1.—Left pectoral fin of specimen 1.
„ 2.—Pectoral fin of *Ceratodus*, after Huxley.
„ 3.—Pelvic fin, after Günther.
„ 4.—Right pelvic fin of specimen 1.
„ 5.—Left pelvic fin of specimen 1.
„ 6.—Left pelvic fin of specimen 2.
„ 7.—Right pelvic fin of specimen 2.

Notes on the Pleuronectidæ of Port Jackson, with descriptions of two hitherto unobserved species.

By William Macleay, F.L.S., &c.

Fishes of this family are rarely seen in the Sydney Market, and the species most frequently seen and generally known as the "Flounder," cannot, in point of quality as food, be compared with the Turbot, Sole, or other *Pleuronectidæ* of cooler seas. But it by no means follows that, because our fishermen do not catch them, they are really rare or of a quality inferior to the Flat Fish of other parts of the world, indeed I believe that in this Paper I shall be enabled to prove the contrary.